

## Variations in Mediterranean Crossbills *Loxia curvirostra*

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Crossbills *Loxia curvirostra* are suitable subjects for research into speciation because they show considerable variation at the population level. There is an extensive literature, both European and American, and there are different theories about the degree of speciation in some populations. For example, Knox (1976) thinks that *scotica* is a good species, while Eck (1981) believes that only 2 species, *curvirostra* (including *scotica* and *pytyopsittacus*) and *leucoptera* should be recognized.

The curious shape of the bill, according to Tallman & Zusi (1984), may have originated following the lateral prising open of seeds by an ancestral Crossbill. This might have favoured the evolution of asymmetrical mandibles through an asymmetrical enlarging of the depressor mandibulae muscle, and the retro-articular process of the lower jaw (an adaptive and mutative complex that is also found in some *Carduelis* – Raikow 1978). This bill structure permits very efficient extraction of seeds from cones.

The aims of my research were as follows: (1) to carry out a biometric analysis of the different Mediterranean populations, in order to examine their relationships with those of North Europe; (2) to establish the extent of variation of the bill in the populations which feed only on pine trees; and (3) to carry out a colour analysis of the populations to investigate the geographic variation.

### MATERIALS AND METHODS

I examined the skins of 200 males and 123 females from museums at Tring (BMNH), Paris (MHNP), New York (AMNH), Milan (MSNM), Palermo (MZP) and Terrasini (MCT), and from the private collection of A. Priolo in Catania (see Acknowledgements). The North European skins came from the breeding areas of W Russia and Finland; the French skins originated both from the breeding areas (central Massif, Alps and Pyrenees) and from Normandy and Brittany (50% of the skins), where the species does not breed (Yeatman 1976, Guermer & Monnat 1980) – they were obtained during the 1929–30 irruption. The North Italian skins came from eastern alpine and subalpine localities and represent both breeding and local migratory birds. The Calabrian skins are those referred to by Moltoni (1964) and were obtained by A. Pazzuconi between 1960 and 1963 in the pine woods of the Sila. Skins from island populations originated from typical breeding localities in Mallorca, Corsica, Sicily and Cyprus. The North African birds came from Tunisia, Algeria and Morocco. I also examined a few juvenile specimens of each population.

The following measurements were taken: flattened wing, tarsus and tail lengths according to Svensson (1975), upper mandible length from the

TABLE 1

Numbers of skins of Crossbills *Loxia curvirostra* examined arranged by month of year.

	MONTH												
	J	F	M	A	M	J	J	A	S	O	N	D	unknown
N-E (65)	2	5	5	2	8	7	1	5	6	3	4	12	5
F (42)	-	-	-	3	3	-	5	8	1	9	8	3	2
N-I (43)	3	6	-	-	3	-	2	4	4	11	3	7	4
CA (23)	3	2	3	-	-	-	4	2	5	-	1	3	-
SI (12)	2	2	-	-	3	2	-	-	-	1	-	2	-
N-A (70)	6	8	5	22	6	-	-	-	1	17	5	-	-
CO (8)	-	-	-	1	2	-	-	-	3	-	1	-	1
MA (25)	1	11	1	5	-	-	2	-	-	2	-	1	2
CY (35)	1	-	-	12	-	7	-	1	10	-	-	4	-

N-E=North Europe; F=France; N-I=North Italy; CA=Calabria; SI=Sicily; N-A=North Africa; CO=Corsica; MA=Mallorca; CY=Cyprus. In brackets the sample size (both sexes).

feathering to tip (bill length), and bill depth at the base. Because of the difficulties in taking accurate tail lengths from skins (cf. Eck 1981), I did not use this measurement for comparisons. The index of curvature of the bill was calculated for each bird by the method described by Knox (1976). This index gives a measure of the steepness of the curvature of the culmen.

The AMNH skins were examined for me by Renato Massa, some BMNH skins also by R. Massa and by Carlo Violani. Working together with Fabio Lo Valvo, the shade of colour on the rump and breast of males was measured using the Munsell method (Smithe 1975).

Finally I noted the extent of primary moult and the general condition of the plumage (worn/abraded), following Ginn & Melville's (1983) method. Depending on the state of growth of each new primary, the primary moult score ranges from 1 to 5, i.e. from earliest to final development; hence the maximum score for 9 primaries at the end of the moult is 45.

I considered that the specimens examined were nearly all adults. According to Tordoff (1952) and Herremans (1982), the unworn secondary coverts of immature birds are white-tipped and the tail feathers are pointed and worn, whereas those of adults are rounded; but both authors agree on the difficulty of separating some immature birds from adults.

Table 1 lists the numbers of skins examined arranged by month of year. Appendix 1 summarises the distribution of Crossbills in the Mediterranean area.

## RESULTS

### Biometrics of the Mediterranean Crossbills

The biometrics of the Crossbills examined are given in Table 2 and Fig. 1 compares the data for different pairs of adjacent populations. My results from North Europe, North Africa and Cyprus are very similar to those published by Knox (1976), particularly for the index of curvature (with the exception of Cyprus females). The wing lengths of Cyprus males are rather different; Knox (1976) gives 97.5 mm for 15 birds against 95.9 mm for my 22 birds. The measurements made from live individuals caught in Belgium during the 1979 irruption, probably coming from a North European

TABLE 2  
Biometrics (mm) of Crossbills *Loxia curvirostra*.

		MALES				FEMALES					
		b-l	b-d	t-l	w-l	i.c. (-400)	b-l	b-d	t-l	w-l	i.c. (-400)
North Europe	n=35	19.04	11.34	17.35	97.7	42.5*	18.82	11.0	16.79	95.2	46.2*
		(17.2-20.4)	(10.8-12.8)	(15.8-19.7)	(95.0-103.5)	(8-74)	(17.0-19.7)	(9.8-12.3)	(15.0-19.6)	(90.1-98.0)	(22-68)
France	n=28	18.04	11.69	18.07	95.86	-	17.17	11.4	16.78	93.35	-
		(16.3-19.8)	(11.0-12.5)	(16.6-19.3)	(91.3-101.0)	-	(16.0-18.6)	(11.0-12.2)	(15.6-19.0)	(90.3-96.5)	-
North Italy	n=25	19.66	11.51	17.92	96.33	43.7	19.09	11.29	17.52	92.13	45.14
		(18.3-21.0)	(10.7-12.1)	(16.9-21.6)	(90.0-99.7)	(26-87)	(17.6-20.8)	(10.0-12.2)	(16.0-19.8)	(85.7-96.6)	(28-91)
Calabria	n=19	19.5	11.65	18.07	96.68	54.7	19.87	11.24	17.8	94.43	-
		(17.6-22.6)	(10.5-12.6)	(16.0-19.6)	(91.9-100.0)	(22-90)	(18.8-21.0)	(10.7-11.9)	(17.1-18.4)	(92.1-95.7)	(35-50)
Sicily	n=8	19.78	11.73	17.79	95.83	52.7	19.95	11.17	17.97	92.14	-
		(18.5-21.0)	(11.2-12.1)	(16.9-19.0)	(92.0-97.4)	(37-70)	(19.2-20.4)	(10.7-11.9)	(16.8-18.6)	(89.7-93.4)	(18-53)
North Africa	n=41	19.22	11.71	17.61	95.86	68.8	18.43	11.29	17.25	94.0	63.5
		(17.5-22.3)	(10.6-12.7)	(15.0-21.0)	(89.0-103.0)	(22-88)	(15.0-19.9)	(9.5-12.4)	(15.0-19.0)	(87.0-98.6)	(34-100)
Corsica	n=5	18.94	11.68	17.69	96.46	-	18.98	11.53	16.34	91.63	-
		(17.4-20.6)	(11.0-12.5)	(16.7-19.1)	(93.0-98.0)	(45-50)	(18.1-19.8)	(11.3-12.0)	(15.0-17.3)	(89.0-95.9)	(30-50)
Mallorca	n=17	17.82	11.22	17.37	91.31	55.7	17.67	11.05	17.29	90.74	50.3
		(16.4-19.6)	(10.2-12.2)	(15.9-19.0)	(86.0-95.0)	(35-85)	(16.8-18.3)	(10.3-12.2)	(16.1-18.5)	(88.4-92.0)	(25-77)
Cyprus	n=22	20.27	12.37	18.48	95.95	76.7	18.8	11.87	18.95	92.57	82.2
		(18.7-21.9)	(11.6-13.3)	(15.9-21.0)	(92.0-101)	(60-108)	(14.9-21.5)	(10.8-13.0)	(18.0-21.0)	(89.0-97.3)	(70-99)

Mean, standard deviation and range of variation (in brackets). \* = from Knox (1976). b-l = bill length, b-d = bill depth, t-l = tarsus length, w-l = wing length, i.c. (-400) = index of bill curvature according to Knox's (1976) method. n is the sample size for all the parameters, excluding i.c. for N-A, CO and MA, which are respectively 21, 2 and 9 in males and for N-A and CY in females are 13 and 6 respectively.

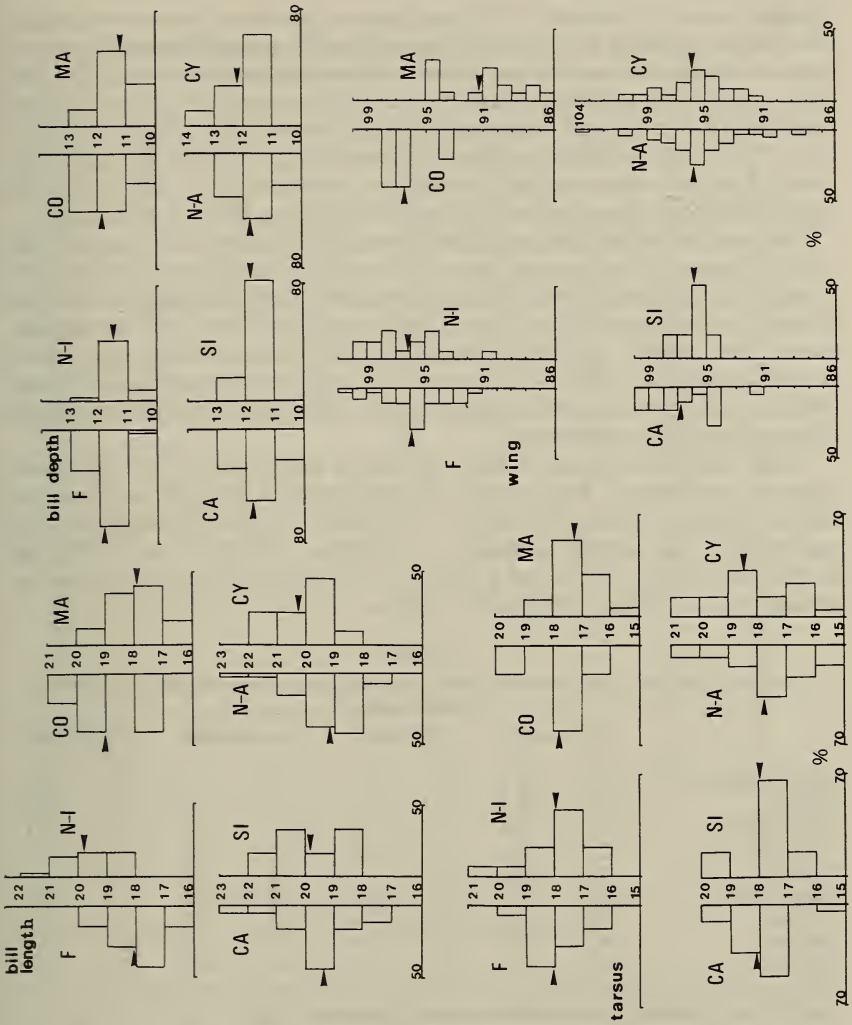


Figure 1. Bill length and depth, tarsus length and wing length of adjacent geographical populations of male Crossbills *Loxia curvirostris* expressed as a percentage per 1 mm of total measured (mm). The arrow shows the average value (see also Table 2).

F=France;  
 N-I=North Italy;  
 CO=Corsica;  
 MA=Mallorca;  
 CA=Calabria;  
 SI=Sicily;  
 N-A=North Africa;  
 CY=Cyprus.

breeding area (Herremans 1982), are greater than mine (male wing length 100.29 mm, females 97.36 mm). There is usually some difference between biometrics taken from live specimens and from skins (Svensson 1975), but this would fail to account for a difference of this magnitude. There is clinal variation of wing length from east to west across Russia (Vaurie 1956, *in* Knox 1975). We probably examined different samples of this variation. My North Europe values, on the contrary, are very similar to those taken by Eck (1981) from skins (male wing length 97.03 mm, females 94.72 mm).

The smallest individuals examined came from Mallorca, the largest from North Europe. The greatest index of curvature came from Cyprus and North African specimens. The measurements from the Calabro-Sicilian population fell between the North Italian and the North African populations. The French specimens show unusual characteristics; they were caught during the 1929-30 irruption and represent a population whose origin is unknown, since the sample appeared different from that of North Europe for all the parameters.

Wing length decreases, while bill length and index of bill curvature increase southwards. Regressions of wing length, bill length and index of bill curvature at different latitudes are significant (French specimens were excluded): wing length-latitude:  $y = 0.083x + 92.22$ ;  $P = 0.024$ ; bill length-latitude:  $y = -0.013x + 19.85$ ;  $P = 0.024$ ; index of bill curvature-latitude:  $y = -0.854x + 92.75$ ;  $P = 0.025$ .

TABLE 3  
Percent difference of biometrics of some Crossbill *Loxia curvirostra* populations from North Europe.

	Bill length		Bill depth		Tarsus length		Wing length	
	m	f	m	f	m	f	m	f
Great Britain*	-0.7	-2.8	0.5	0	-	-	-0.9	2.9
France	-7.3	-8.8	3.1	3.7	4.1	-0.1	-1.9	0.9
North-Italy	3.2	1.4	1.5	2.6	3.3	4.3	-1.5	-0.4
Calabria	2.4	5.6	2.7	2.1	4.1	6.0	-1.1	2.1
Sicily	2.6	6.0	2.7	1.5	0.6	7.0	-2.2	-1.5
North-Africa	0.9	-2.1	3.3	2.6	1.5	2.7	-1.9	1.7
Corsica	-0.6	0.8	3.0	4.8	1.9	-2.7	-1.3	-0.1
Mallorca	-6.5	-6.2	-1.1	0.4	0.1	3.0	-6.6	-2.0
Cyprus	6.5	-0.2	8.2	7.9	6.5	12.9	-2.1	0.1

m=males; f=females; \*=from measurements of Marquiss (1980)

Table 3 shows the percentage difference of each population compared to the North European specimens. All the Mediterranean populations, apart from that of Mallorca, have more curved and deeper bills and longer tarsi than the North European ones. I found a significant correlation between bill length and depth in all the populations ( $r_s = 0.65$ ;  $P < 0.05$ ).

Table 4 shows the significant differences obtained by student t-test between the biometric parameters of pairs of populations (see also Fig. 1). Since the female sample was too small, I compared only biometrics of males. The Table shows a significant difference between many pairs of populations, particularly for some parameters such as the bill length and the index of curvature. Samples from Cyprus and Mallorca were

TABLE 4

Statistical levels of probability of the biometric parameters of pairs of populations assessed by Student t-test in samples of Crossbills *Loxia curvirostra* examined.

	F	N.I.	CA	SI	N.A.	CO	MA	CY
b.l.	.001	.02	N.S.	N.S.	N.S.	N.S.	.001	.001
b.d.	.01	N.S.	N.S.	N.S.	.01	N.S.	N.S.	.001
t.l.	.001	.05	.01	N.S.	N.S.	N.S.	N.S.	.001
w.l.	.01	.05	N.S.	.05	.01	N.S.	.001	.01
i.c.	-	N.S.	.001	.05	.001	-	.01	.001
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b.l.		.001	.001	.001	.001	N.S.	N.S.	.001
b.d.		N.S.	N.S.	N.S.	N.S.	N.S.	.01	.001
t.l.		N.S.	N.S.	N.S.	N.S.	N.S.	.01	N.S.
w.l.		N.S.	N.S.	N.S.	N.S.	N.S.	.001	N.S.
<hr/>								
b.l.			N.S.	N.S.	.001	N.S.	N.S.	.05
b.d.			N.S.	N.S.	N.S.	N.S.	.05	.001
t.l.			N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
w.l.			N.S.	N.S.	N.S.	N.S.	.001	N.S.
i.c.			N.S.	N.S.	.001	-	N.S.	.001
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b.l.				N.S.	N.S.	N.S.	.001	.05
b.d.				N.S.	N.S.	N.S.	.02	.01
t.l.				N.S.	N.S.	N.S.	.02	N.S.
w.l.				N.S.	N.S.	N.S.	.001	N.S.
i.c.				N.S.	.05	-	N.S.	.01
<hr/>								
b.l.					N.S.	N.S.	.001	N.S.
b.d.					N.S.	N.S.	.05	.05
t.l.					N.S.	N.S.	N.S.	N.S.
w.l.					N.S.	N.S.	.001	N.S.
i.c.					N.S.	-	N.S.	.01
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b.l.						N.S.	.001	.001
b.d.						N.S.	.01	.001
t.l.						N.S.	N.S.	.02
w.l.						N.S.	.001	N.S.
i.c.						-	N.S.	N.S.
<hr/>								
b.l.							.05	.01
b.d.							.01	.05
t.l.							N.S.	N.S.
w.l.							.001	N.S.
<hr/>								
b.l.								.001
b.d.								.001
t.l.								.01
w.l.								.001
i.c.								.02

Abbreviations as in Table 2. N.S. = Not significant. (See Table 2 for abbreviations.)

statistically different from other samples for 3 parameters of the 5 analysed. Inexplicably, the French sample appeared different from that of North Europe for all the parameters.

Finally I found a small sexual dimorphism in all the biometrics of each population. Males were larger than females by a ratio of 1.02 to 1.

### The colour of the Mediterranean Crossbills

According to some authors (Griscom 1937, Bannerman & Bannerman 1958, Thibault 1983), the males of Mediterranean Crossbills are less red and the females less green than North European ones, but no direct measurements have been made previously. We found 23 different shades of yellow, orange and red in the males (5 shades of yellow: numbers 153, 57, 53, 56 and 52 in the tables of Smithe (1975); 6 of orange: numbers 6, 18, 132D, 132C, 17 and 16; and 12 of red: numbers 10, 94, 15, 13, 14, 210, 12, 11,

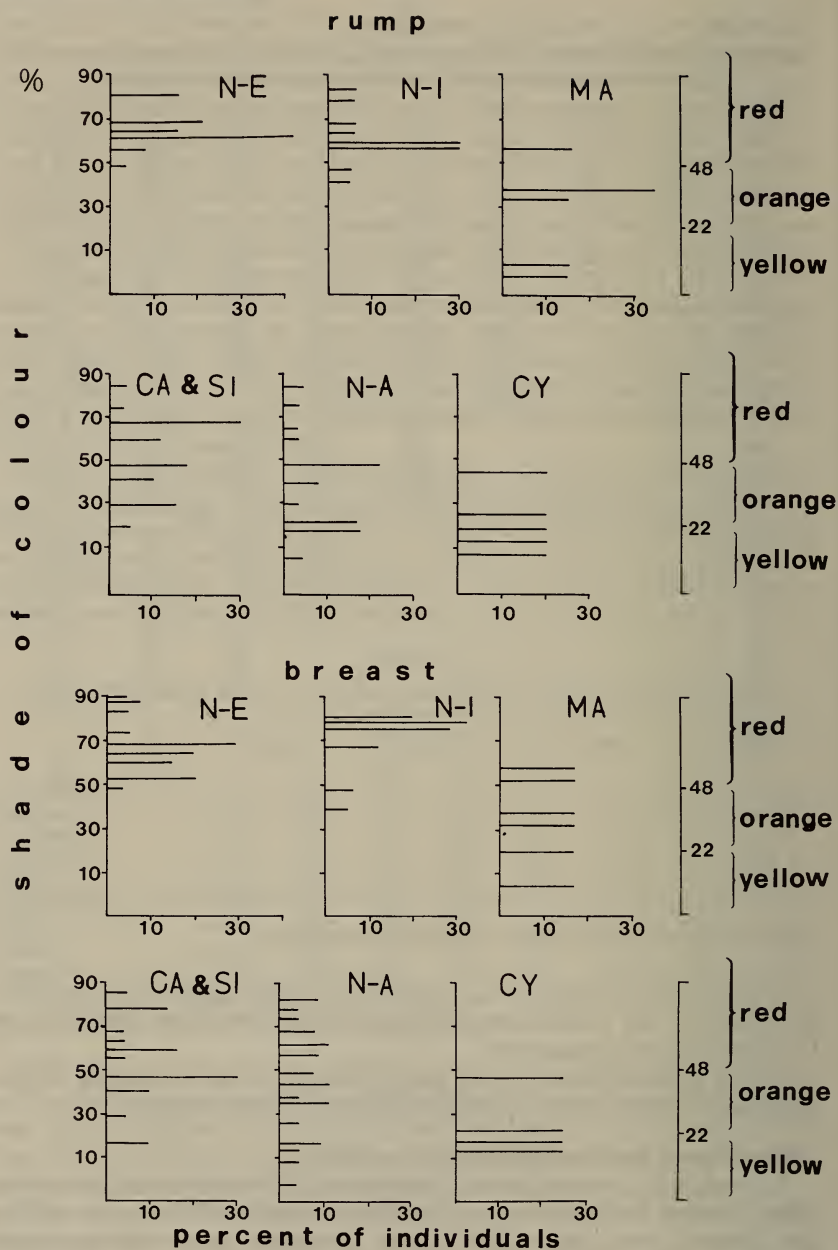


Figure 2. Percent average values of breast and rump colour of male Crossbills *Loxia curvirostra* ranged into shades of yellow (between 0 and 22%), orange (between 22 and 48%) and red (more than 48%).

108A, 108, 8 and 7). I calculated the percent values of these colours, e.g. colour 18, which is seventh between yellow and red, represents  $7/23 \times 100 = 30.4\%$ . Fig. 2 shows the results. Shades of yellow fell between 0 and 22%, shades of orange between 22 and 48%, and red was more than 48%.

To examine the effect of wear, I compared the colour of North African samples from April and October, but found no significant difference (av. = 33.3 and 32.9%). There is clinal variation in the shade of plumage colour; males with reddish plumage are more common in North Europe, whereas in the Mediterranean area yellowish individuals are more frequent. Table 5 shows the percent average values ( $\pm$  s.d.) of colours for the breast and rump. Regression of the average colour values at different latitudes is significant for the breast and rump ( $y = 1.072x + 0.546$ ;  $P = 0.025$ ). In the analysis, birds from Calabria and Sicily were grouped together. The small sample from Corsica was not analysed. The Mallorca and Cyprus populations were less intensely coloured than others at the same latitude, perhaps due to isolation.

TABLE 5

Percent average ( $\pm$  s.d.) of shade of colours between yellow and red in the breast and rump of the examined skins of Crossbills *Loxia curvirostra* - see text. (See Table 2 for abbreviations.)

	N-E	N-I	MA	CA & SI	N-A	CY
BREAST	66.14 $\pm$ 10.7	65.0 $\pm$ 10.2	44.0 $\pm$ 20.4	54.13 $\pm$ 18.4	46.4 $\pm$ 23.0	25.0 $\pm$ 15.8
RUMP	65.3 $\pm$ 6.6	63.7 $\pm$ 8.4	38.3 $\pm$ 23.0	53.2 $\pm$ 17.9	41.1 $\pm$ 22.8	20.8 $\pm$ 13.3

### Breeding and moult

Although many individuals moult between July and November (see e.g. Tordoff 1952, Ginn & Melville 1983, Busse 1984), at least some North European populations moult irregularly. Herremans (1982) found adults with complete, active and suspended moult during the 1979-80 irruption in Belgium, between September and October. However, it seems that breeding cycles of Mediterranean Crossbills are less irregular. Nesting begins in winter or early spring and lasts until early summer. Some breeding throughout the rest of the year is known, but it is not common (e.g. Heim de Balsac & Mayaud 1962, Flint & Stewart 1983, Thibault 1983).

Based on the skins that I examined, breeding begins in winter (juveniles from January), with a peak in February and March. It seems that the breeding cycle is quite regular, perhaps due to the regular availability of food in the Mediterranean pine woods. According to Eck (1981), there is no evidence that the Mediterranean Crossbills are sedentary, but in my opinion it seems quite likely. The North African populations are also believed to be sedentary (M. Thévenot).

The breeding cycle ends between April and May, by which time the adults show abraded plumage. Crossbills then moult regularly between May and September. I did not find any suspended moult during this period. The state of moult of the specimens examined according to Ginn & Melville's (1983) method was as follows:-

*Mallorca.* The only 2 summer specimens examined (July) had primary



scores of 19 and 33. Two specimens from October were in fresh plumage.

*Corsica*. September skins were in fresh plumage.

*Calabria*. Four July skins: primary scores of c. 20; one from August had completed its moult, another had a score of 40. Five specimens from September: one with a completed moult, the others with scores of 39, 42, 44 and 44 (completed moult). I found fresh plumage on all specimens caught between November and March.

*Sicily*. Three specimens from May were just starting moult (scores: 8, 10 and 12); two in June scored 20 and 23; one in October and 2 in December were in fresh plumage.

*North Africa*. The autumn skins were all in fresh plumage, with no trace of moult. I did not examine any summer skins, but it seems likely that birds moult between June and September, in common with the other populations considered in this study.

*Cyprus*. I found scores between 23 and 31 in the June skins. Specimens caught in August and September had almost completed their moult (scores between 38 and 42).

## DISCUSSION

### Bergmann's and Allen's rules

In order to understand more fully the problems of Crossbill taxonomy, a detailed examination of variation along 2 other Mediterranean peninsulas, Iberia and the Balkans, and along the Maghreb, from Tunisia to Morocco, will be necessary.

Phillips (1977) thinks that Crossbills violate all the ecological rules, including Bergmann's; but according to Griscom (1937) the decrease of Crossbill body size southwards does not occur in the New World (Phillips's populations), but does so in the Palaearctic.

Many researchers use wing-length as a measure of body size for Bergmann's rule and bill-length for Allen's. Northern populations generally have longer wings than any of the Mediterranean ones and the wing-lengths of *scotica* and *pytyopsittacus* conform with this (Knox 1976), thereby observing Bergmann's rule. It could be that *balearica* and *guille-mardi* have shorter wings due to the effect of insularity. However, large southern populations (e.g. in North Africa) also have shorter winglengths. Hence my figures support Griscom (1937) that in the Palaearctic the body size of Crossbills decreases southwards.

Turning now to Allen's rule, the bills of Mediterranean Crossbill populations are longer and larger than those of northern ones. Significant regressions of bill length and index of curvature at different latitudes suggest that Crossbills do not violate Allen's rule.

Adkisson (1977) also found similar clinal variation of wing and bill lengths in a related species, the Pine Grosbeak *Pinicola enucleator*, in North America.

### Adaptive character

Crossbills with a slender bill feed on several conifer species, whereas those with a strong bill feed only on pines (see Appendix 1). Pine cones are

larger than cones of other conifers and the bill size and strength of a Crossbill should be a good indication of its power.

I measured the length of the cone scales of *Pinus nigra* from Cyprus and Calabria, *P. laricio* from Sicily and *P. halepensis* from Tunisia and Mallorca and I found respectively the following values: 27.3 mm  $\pm$  1.5 (n=40), 21.5  $\pm$  3.6 (n=23), 22  $\pm$  1.5 (n=56), 23.02  $\pm$  2.5 (n=27) and 23.08  $\pm$  3 (n=27). They correlated with the index of curvature for the respective populations (for the males  $r_5 = 0.86$ ;  $P < 0.05$ ). This correlation agrees with the hypothesis that the bill size is an adaptive character for feeding on pine cones. If so, the clinal variation of bill according to Allen's rule, could be casual.

### Gene flow

Clinal variation in size and colour in Crossbills is an indication of gene flow between populations, brought about by irruptions from northern Europe. Speciation frequently takes place following geographic differentiation, interpreted as genetic change in response to environmental variations. In these instances, the peripheral populations show a greater disposition to speciation (Mayr 1963). In fact we find the most differentiated forms are in the north (*scotica* and *pytyopsittacus*), and in the south (the Mediterranean populations). Possibly the rate of speciation has been accelerated by the development of sedentary populations.

I agree with Eck's (1981) hypothesis of a centrifugal spread from the central European populations northwards and southwards, producing forms with strong bills. These forms probably became sedentary. We know of only a few irruptions by *pytyopsittacus* (Catley & Hursthouse 1985), and none by Mediterranean forms. The variation of Mediterranean populations may be the result of different immigrations from different European populations, whose range of variation is wide (Griscom 1937).

To judge from the morphological variation seen in Crossbills (Tables 2-6), there may still be gene flow between central-northern and Mediterranean populations, though for some populations it may be scarce or even absent. I think, for instance, the process of speciation is advanced in the populations in Cyprus, Mallorca and North Africa, but less so in Calabria, Sicily and Corsica. Whereas for the former 3 countries trinomial distinction is useful, for the latter 3 it is meaningless.

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